

Motion adaptation and attention: A critical review and meta-analysis

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Motion adaptation and attention: A critical review and meta-analysis.

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The motion aftereffect (MAE) provides a behavioural probe into the mechanisms underlying
motion perception, and has been used to study the effects of attention on motion processing.
Visual attention can enhance detection and discrimination of selected visual signals.
However, the relationship between attention and motion processing remains contentious: not
all studies find that attention increases MAEs. Our meta-analysis reveals several factors that
explain superficially discrepant findings.

Across studies (37 independent samples, 76 effects) motion adaptation was significantly and
substantially enhanced by attention (Cohen's $d=1.12$, $p<.0001$). The effect more than doubled
when adapting to translating (vs. expanding or rotating) motion. Other factors affecting the
attention-MAE relationship included stimulus size, eccentricity and speed. By considering
these behavioural analyses alongside neurophysiological work, we conclude that feature-
based (rather than spatial, or object-based) attention is the biggest driver of sensory
adaptation.

Comparisons between naïve and non-naïve observers, different response paradigms, and
assessment of 'file-drawer effects' indicate that neither response bias nor publication bias are
likely to have significantly inflated the estimated effect of attention.

Keywords:

Attention, motion adaptation, motion aftereffect, systematic review, meta-analysis

1. Background

Attention refers to our ability to selectively process certain aspects of a visual scene, such that particular regions or features are enhanced, and irrelevant stimuli are inhibited (Carrasco, 2011). The effects of attention on perceptual processes are usually measured via manipulations of covert attention in which attention is directed independently of eye movements. This contrasts with overt attention, in which a redirection of attention is accompanied by an eye movement to fixate the attended region. Covert spatial attention enhances signals from the attended location, reducing noise, and changing decision criteria (see Carrasco, 2011 for an overview), and has been shown to operate at all levels of the visual hierarchy, even early visual areas previously believed to be pre-attentive and entirely sensory, i.e. the primary visual cortex (V1) (e.g. Silver et al., 2007; Somers et al., 1999). Whether such attentional effects generalize to motion processing, however, remains contentious. Here we consider evidence for the influence of covert attention on motion processing, as evidenced by effects of attention on motion adaptation.

The relationship between attention and visual motion processing has been studied since the early 20th century. Wertheimer (1912/1961) found that attention altered the perceived motion direction of ambiguous apparent motion, a finding supported by more recent work (Kohler, Haddad, Singer, & Muckli, 2008). In addition, researchers have found that the perceived direction of third-order motion (the motion of important visual details, i.e. the ‘figure’ is separated from the ‘ground’ within a salience map; Lu and Sperling, 2001) can be determined entirely by attention (Lu and Sperling, 1995). The observed effect of attention on higher-level motion processes is in keeping with the notion that attention exerts a greater influence in more advanced regions of the cortical visual hierarchy (Carrasco, 2011). However, the picture is less clear when we consider low-level (first-order / luminance-defined) motion.

The effect of attention on luminance-defined motion processing has been probed behaviourally via the motion after-effect (MAE): following prolonged inspection of a moving stimulus, illusory motion is perceived in the opposite direction. Descriptions of the MAE date back to Aristotle, and it was popularised by Addams (1834) as the ‘the waterfall effect’. After-effects have earned the label of the “psychologist’s microelectrode” (Frisby, 1979) and the MAE is viewed as a powerful research tool for probing motion-sensitive mechanisms (see Fig. 1a).

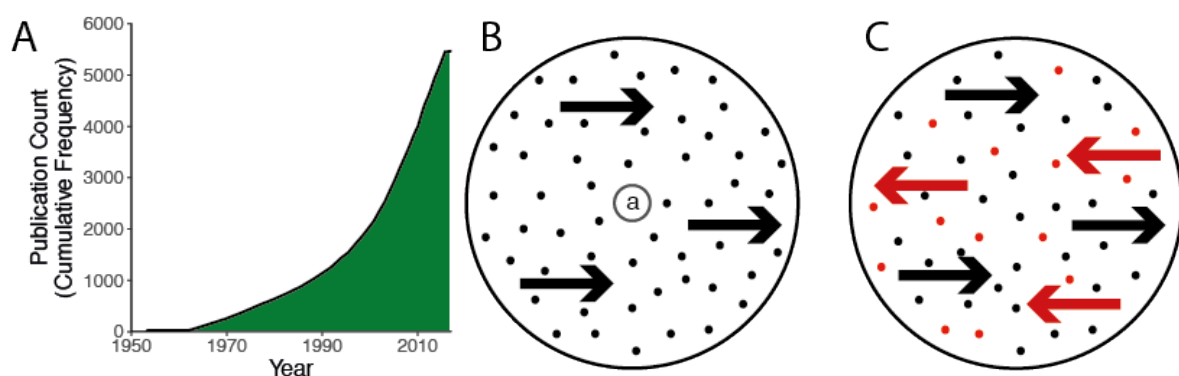


Fig. 1. (a) Cumulative frequency of publications related to the motion aftereffect. A PubMed search (keywords: motion aftereffect OR motion adaptation) revealed 5470 publications since 1950. (b & c) A schematic of typical paradigms used to measure the effect of covert attention on motion adaptation. (b) A moving stimulus is presented within an annulus. To manipulate attention, a centrally presented stimulus such as a stream of letters is fixated, while observers perform either a difficult / high-load task, or an easy / low-load task, or passively view the stimulus. (c) The motion tracking paradigm: two populations of dots (indicated here by different colours) each follow a different motion trajectory. Observers attend to one of the two superimposed motion patterns.

If basic motion mechanisms are affected by spatial attention, we expect to find larger MAEs when attention is directed towards, rather than away from a moving adaptation stimulus. However, in an influential paper exploring the MAE, Wohlgenuth (1911) reported

that diverting attention to a central rapid serial visual presentation (RSVP) task had no effect on adaptation to a spiral motion stimulus, leading to a long-held view that the mechanisms responsible for motion adaptation are pre-attentive. Indeed, some recent papers continue to endorse this view (Morgan, 2013, 2012, 2011). This suggestion – that motion adaptation is independent of attention - is aligned with previous reports that adaptation to other simple visual features (spatial frequency, orientation) is unaffected by attention or awareness (Blake & Fox, 1974; He, Cavanagh, & Intriligator, 1996).

A landmark study by Chaudhuri (1990) challenged this pervasive view. Observers viewed a large moving stimulus for 60 seconds. During this adaptation period, numbers and letters appeared within a small central aperture and observers either engaged in a demanding alphanumeric task, or passively viewed the stimulus (see Fig. 1b). Observers subsequently viewed a static stimulus and reported the MAE duration. Attending to the central task caused a substantial reduction in the duration of the subsequent motion after-effect. Subsequently, multiple studies have similarly found that diverting attention away from a moving adaptor reduces the duration (e.g. Chaudhuri, 1990; Rezec, Krekelberg, & Dobkins, 2004) or velocity of the subsequent MAE (e.g. Georgiades & Harris, 2000a; Taya, Adams, Graf, & Lavie, 2009).

In broad agreement with this behavioural data, neuroimaging evidence suggests that, under similar attentional manipulations, motion-related activity in medial temporal (MT) / medial superior temporal (MST) areas is modulated by attention (Beauchamp et al., 1997; Rees et al., 1997). Load theory of selective attention suggests that during a demanding task, limited resources are available to process task-irrelevant information (such as a peripheral motion stimulus). Conversely, a low-load task requiring fewer resources leads to greater processing of task irrelevant stimuli (Lavie, 2005). Rees, Frith, & Lavie (1997) presented irrelevant expanding motion in the periphery and words at fixation. In line with attentional

load theory, a low load task (detect uppercase words) resulted in increased activation across several areas (MT, V1/V2 and the superior colliculus) and longer MAE durations, relative to a high-load task (detect bisyllabic words).

A clear consensus on whether (or under what conditions) attention increases motion adaptation is yet to emerge, however, due to null (Morgan, 2013, 2012, 2011; Pavan and Greenlee, 2015), or inconsistent findings (e.g. Georgiades & Harris, 2002b; Takeuchi & Kita, 1994). One might argue that, given the importance of motion for fundamental tasks such as segmentation (including breaking camouflage), depth perception and guiding self-motion (e.g. Gibson, 1958; Nakayama, 1985), it would be evolutionarily advantageous if motion were processed independently of attention. Certainly, motion is a powerful cue for pop-out in visual search (Driver et al., 1992; Nakayama and Silverman, 1986). If motion adaptation mechanisms are pre-attentive, why have many studies reported an effect of attention on MAEs? One suggestion is that affirmative findings reflect response bias: observers expect weaker MAEs to follow diverted-attention conditions and bias their responses accordingly. Measures of MAE duration (as used by Chaudhuri, 1990 and others) may be particularly susceptible to bias / criterion effects because observers struggle to determine the point at which the MAE has completely disappeared (Morgan, 2012; Blake & Hiris, 1993).

Other factors, such as the choice of stimuli and experimental paradigm almost certainly contribute to variability across the findings from different studies. Paradigms differ in the extent to which the attentional manipulations direct spatial, featural and surface / object-based attention. As reviewed below (see section 1.2.1.1), a coherently translating stimulus may recruit feature-based attention more effectively than complex (rotating and /or expanding) stimuli. Others have demonstrated that the eccentricity of the adaptor (Georgiades and Harris, 2000a, 2000b) and the type of test stimulus (static vs. dynamic; Culham, Verstraten, Ashida, & Cavanagh, 2000) may modulate the effect of attention. Attentional

tracking paradigms, in which observers attend one of two superimposed motion stimuli (e.g. Lankheet & Verstraten, 1995; Mukai & Watanabe, 2001; see Fig. 1c) may reveal larger attentional effects than those that direct attention towards or away from the location of a single motion stimulus (Morgan, 2011). A meta-analysis allows us to evaluate all of these factors and others (as detailed in Section 1.2) such that we can better understand whether, and under what conditions, motion processing (and motion adaptation) is modulated by attention.

1.1. The current review: justification and objectives

In contrast to single empirical papers, or selective, narrative reviews (e.g. Burr & Thompson, 2011), our meta-analysis provides sufficient power to quantify the effects of multiple factors on the attention-motion relationship. We assess the effects of varying the adaptation stimulus (translation vs. complex motion, size, eccentricity, speed and duration), the test stimulus (static vs. dynamic), the experimental paradigm (MAE duration vs. strength/speed, 2AFC vs. matching, attentional tracking vs. distraction) and participant characteristics (naïve vs. non-naïve).

1.2. Factors that may affect the relationship between attention and motion processing

1.2.1. Characteristics of the adaptation stimulus

1.2.1.1. Type of motion

The effect of attention on neural responses to motion stimuli may depend on the type of motion being presented. Spatial attention has been shown to increase the overall response gain of MT neurons corresponding to the attended region (Treue and Martínez-Trujillo, 1999). In contrast, feature-based attention has a substantial direction-specific effect, such that neurons in V1, MT and MST tuned to the attended motion direction show a response gain, while neurons tuned to the opposite direction are suppressed (Saproo and Serences, 2014;

Treue and Martínez-Trujillo, 1999; Treue and Maunsell, 1996). Importantly, this effect of feature-based attention spreads across the visual field, such that attending to leftward motion in one location will enhance processing of leftward motion across all retinal locations. One would expect this direction-specific modulation of neural activation to have a large role in the enhancement of MAEs. When observers attend to a large, coherently translating stimulus (vs. central letters, for example), spatial and feature-based attention will combine (Treue and Martínez-Trujillo, 1999) to enhance the neural representation of the moving stimulus across multiple motion-sensitive cortical regions.

In contrast to translating stimuli, rotating or expanding motion patterns are composed of local motion signals whose directions vary as a function of position (Carrasco, 2011). Attending to these complex motion stimuli will not, therefore, enhance V1/MT activity via simple feature-based attention mechanisms. However, there is now evidence from neurophysiology (Wannig et al., 2007) and fMRI (Kamitani and Tong, 2006) that surface, or object-based attention can enhance V1 and MT activation as a function of both direction and position, when more complex motion patterns are attended. These effects could be driven by feedback from the dorsal section of MST (MSTd), an area known to have larger and more complex receptive fields that have been implicated in optic flow processing (Graziano et al., 1994; Saito et al., 1986; Tanaka and Saito, 1989).

Behavioural studies of attention and motion processing often assume, implicitly, that increased motion-related activation (due to attention) can be inferred from changes in adaptation. However, adaptation effects may vary across regions. Following prolonged activation, V1 neurons show substantial reductions in responsiveness and sensitivity to motion directions close to the adapted direction. However, reductions in responsivity in MT are much smaller (Kohn and Movshon, 2004, 2003). Thus, differences in adaptation across the cortex, in addition to variations in the effects of spatial, featural and surface-based

attention on neural responses to translating vs. complex motion patterns, strongly suggest that the effect of attention on adaptation will depend on the type of motion stimulus.

1.2.1.2. Size of adaptation stimuli

Previous studies have asked whether stimulus size determines the extent of attentional modulation (Georgiades and Harris, 2000b; Takeuchi and Kita, 1994). If attentional effects are larger at higher-level cortical regions (at least for complex motion) then attentional modulation of MAEs might increase with stimulus size, given increasing receptive field size from V1 to MT and MST (Smith et al., 2001). On the other hand, it may be easier to shift spatial attention away from a smaller stimulus, particularly as its distance from the task-relevant stimulus increases.

1.2.1.3. Eccentricity of adaptation stimuli

Most paradigms used to explore the attention-motion relationship use an attentional task related to a central stimulus to draw attention away from a peripheral motion stimulus. One might expect that when the adaptation stimulus is close to the distracting stimulus, attentional resources may ‘spill over’ to the motion stimulus more easily. A key component of the load theory of attention is that the target and distractor must be spatially separated (Lavie, 2005). A demanding task at fixation may reduce the extent to which peripheral distractors are processed, by narrowing the window of spatial attention around the central, task relevant stimuli. Thus, more eccentric adaptation stimuli may reveal larger effects of attentional modulation. Conversely, there is some empirical evidence that attentional modulation is stronger for adaptation stimuli closer to fixation (Georgiades and Harris, 2000a, 2000b).

1.2.1.4. *Speed of adaptation stimuli*

Many studies have considered how motion adaptation varies as a function of adaptor speed, classically reported to follow an inverted U-shape (see Thompson, 1998 for an overview). In terms of attention, Georgiades & Harris (2002b) found that attention modulated motion adaptation for faster adaptation stimuli. However, for slower adaptation stimuli, the effect of attention increased with spatial frequency. The relationship between speed, attention, and motion processing has rarely been examined within studies. However, the wide range of adaptation speeds used across different studies allows us to explore this in the current analysis.

1.2.1.5. *Adaptation duration*

As adaptation duration increases, MAEs increase (Hershenson, 1993). In previous work, we explored how the effects of attention vary across the adaptation period by measuring the MAE at regular intervals during an extended adaptation period (Bartlett et al., 2018). Attention affected the asymptotic MAE magnitude, but not the rate at which it accumulated (i.e. the time constant). This finding is broadly consistent with Takeuchi & Kita (1994), who found that diverted attention led to reduced MAEs across adaptation durations of 20, 40 and 80 seconds.

It could be argued, however, that diverting attention may reduce the rate of adaptation, without affecting the asymptotic point, i.e. at longer durations adaptation is saturated, and will not be further enhanced by attention. Such an effect could account for some null findings in the literature, and aligns with work by Blake and colleagues regarding perceptual awareness: after-effects in motion or spatial frequency are reduced under suppression or crowding for low contrast adaptors only – adaptation reaches saturation at higher contrasts, irrespective of awareness (Blake et al., 2006; Blake and Fox, 1974).

222

223 *1.2.2. Test stimulus characteristics*

224 *1.2.2.1. Static vs. dynamic test stimuli*

225 Motion adaptation can be quantified using static test stimuli (e.g. Chaudhuri, 1990) or
226 dynamic tests, such as random dot motion patterns (e.g. Mukai and Watanabe, 2001; Taya et
227 al., 2009) or counterphase flicker (e.g. Nishida and Ashida, 2000; Rezec et al., 2004). Nishida
228 & Sato (1995) suggested that static test stimuli reflect adaptation to first order motion,
229 whereas dynamic (flicker) tests reveal second order MAEs. Static and dynamic tests may
230 also differ in terms of sensitivity to monocular vs. binocular motion mechanisms (e.g.
231 Nishida & Ashida, 2000), and to storage effects (e.g. Verstraten, Fredericksen, Van Wezel,
232 Lankheet, & Van De Grind, 1996). Using an attentional tracking paradigm (see Fig. 1c),
233 Culham, Verstraten, Ashida, & Cavanagh (2000) reported that attention modulated the MAE
234 only when measured via a dynamic test. In summary, MAEs obtained from static and
235 dynamic test stimuli may reflect different motion mechanisms that are differentially
236 modulated by attention.

237

238 *1.2.3. Experimental paradigm*

239 *1.2.3.1. MAE measurement and response*

240 Many studies have quantified the effects of attention on motion adaptation by asking
241 observers to report the cessation of the (illusory) motion of a static test stimulus, i.e. the MAE
242 duration (Chaudhuri, 1990; Morgan, 2012; Rezec et al., 2004). As noted above, this reporting
243 method has been criticised as susceptible to response bias. Alternatively, MAE magnitude
244 has been quantified via velocity matching (Georgiades and Harris, 2000a). 2AFC designs
245 have also been implemented, in which participants select one of two response options, such
246 as the test stimulus' motion direction (e.g. Kaunitz, Fracasso, & Melcher, 2011; Taya et al.,

2009) or which of two test stimuli was moving faster (Morgan, 2013). Some 2AFC paradigms use nulling techniques in which the percentage of test stimulus dots moving oppositely to the aftereffect (Blake & Hiris, 1993; e.g. Mukai & Watanabe, 2001) or the phase shift of the test (e.g. Culham et al., 2000) is adjusted to counteract the aftereffect. 2AFC / two interval forced choice (2IFC) designs have been considered preferable to duration or matching tasks in terms of minimising response bias (Morgan, 2013).

If our analyses reveal that the reported effects of attention on motion adaptation are larger when measured via duration estimation or velocity matching paradigms, this would suggest that some reported effects have been inflated by response bias.

1.2.3.2. Attentional manipulation

Two distinct methods of manipulating attention have been used in the context of motion adaptation. ‘Distractor’ paradigms involve diverting attention away from a moving adaptation stimulus – usually towards a centrally presented, difficult task (see Fig. 1b). This condition is compared with one in which more attention is deployed to the adaptation stimulus, for example during passive viewing. This paradigm involves spatial attention (the moving adaptor and central task are spatially separated). Depending on the type of motion, it may also involve feature and / or surface based attention, as discussed above. Some would also consider it to involve ‘dimension’ based attention, i.e., attention to motion rather than another visual dimension such as colour or shape, because the central task does not usually rely on motion. Reductions in motion-related activation in V1 and MT/MST have been found when attention is directed to the colour or luminance of a moving stimulus, rather than its motion (Beauchamp et al., 1997; Saproo and Serences, 2014), with corresponding changes in the resultant MAE also reported (Taya et al., 2009).

In contrast, ‘attentional tracking’ paradigms ask subjects to attend to one of two superimposed motion patterns (see Fig. 1c). This relies on feature-based attention: i.e. attention is directed to one motion direction, at the expense of another motion direction. Studies that have used attentional tracking have fairly consistently demonstrated attentional modulation of motion adaptation (e.g. Alais and Blake, 1999; Culham et al., 2000; Lankheet and Verstraten, 1995). Accordingly, it has been suggested that the two paradigms probe distinct attentional mechanisms that vary in their effects on motion processing (Morgan, 2012, 2011).

1.2.4. Participant characteristics

1.2.4.1. Participant naivety

It is often noted that the risk of response bias increases with certain paradigms (as discussed in Section 1.2.3.1), and also with non-naïve observers who may know the research hypotheses. As noted above, there have been claims that some reports of attentional modulation of motion adaptation are not just inflated by, but due to response bias (Morgan, 2013, 2012). Indeed, Morgan (2012) failed to find attentional modulation of motion adaptation with naïve observers. The overall picture, however, is less clear, with other studies finding significant effects within groups of naïve observers (e.g. Chaudhuri, 1990; Patterson et al., 2005).

2. Method

2.1. Inclusion and coding decisions

2.1.1. Inclusion criteria

All studies that met the following criteria were included in the present meta-analysis:

1. The study manipulated attention during motion adaptation and reported the subsequent behavioural motion aftereffect.
2. The stimuli did not differ across attentional manipulations.
3. The study was published in an English language journal on or before August 2016.
4. Participants were healthy human adults – studies using patient populations were excluded.
5. The study was not a re-analysis of existing data
6. Sufficient information was provided in order to estimate an effect size (see section 2.3).
7. Only within subject designs were included, due to well-known issues equating within subject and between subject effect size measurements (Lakens, 2013). This removed 7.32% of effects.

2.1.2. Other coding and inclusion decisions

1. If the study assessed both a low load and a no load (passive) condition, these data were pooled into a single ‘low load’ condition and compared against the high load condition.
2. If the study included a manipulation that was not pertinent to the research questions (e.g. different levels of contrast in the adapting stimulus; Rezec et al., 2004), data were pooled across this manipulation (see Supplementary Material S1 for a full list).
3. In order to reduce un-modelled variability, data from conditions / experiments with atypical presentation conditions were excluded. For example, in studies investigating interocular transfer, only data from conditions in which adaptation and test stimuli were presented to the same eye(s) were included (e.g. Nishida and Ashida, 2000). See

Supplementary Material S1 for a full list of included effects and details regarding excluded conditions.

4. If the study was investigating awareness, we only included the data from conditions where observers were aware of the adapter (e.g. Kaunitz et al., 2011).
5. Only visual manipulations of attention were included; auditory attention conditions were excluded (e.g. Houghton, Macken, & Jones, 2003).

2.2. General search and coding strategies

One of the authors (LB) conducted the search for relevant studies and coded the data, in consultation with all authors. A PubMed database search was first conducted. Subsequently, the reference sections of all relevant studies were examined to identify additional relevant papers. Next, articles citing any of the relevant studies were identified via Google Scholar, and the reference lists of all of these articles were then examined. A summary of the excluded articles and the database search terms are presented in the Supplementary Material S2, according to the ‘Preferred Reporting Items for Systematic reviews and Meta Analysis’ guidelines (PRISMA: Moher, Liberati, Tetzlaff, Altman, & The PRISMA Group, 2009).

2.3. Methods

2.3.1. Effect size metric

Cohen’s d , the standardised difference between means (Cohen, 1977), was used as the effect size index for all outcome measures. A positive value indicates a stronger motion aftereffect following passive or low-load adaptation than diverted or high-load attention during adaptation, or following motion-focused compared to passive viewing.

2.3.2. Standardisers for d

Our primary estimator (86.84% of included effects) of Cohen's d was d_{av} , the difference between means (M_{diff}) standardised by the averaged standard deviation (SD) of the measures (Lakens, 2013):

$$d_{av} = \frac{M_{diff}}{\frac{SD_1 + SD_2}{2}} \quad \text{Equation 1.}$$

This formula is recommended for repeated measures designs where there is no pre-post distinction (e.g. before or after treatment). Because both SD measures are equally good estimators of population variability, averaging the two gives the best estimate (Cumming, 2012). In cases where standard deviations were only reported for multiple levels of an irrelevant experimental variable, these values were pooled to reflect the standard deviation collapsed across these levels (see Supplementary Material S3).

If means and standard deviations were not reported, effect sizes were computed from t , p or F values and the degrees of freedom to give d_{RM} , the difference between means standardised by the standard deviation of the difference scores (Lakens, 2013):

$$d_{RM} = \frac{t}{\sqrt{N}} \times \sqrt{2(1 - r)} \quad \text{Equation 2.}$$

In practice, few effect sizes were calculated using d_{RM} (13.16% of overall). As Equation 2 indicates, this estimate corrects for the paired correlation (r) between conditions. These correlations were calculated using equations reported by Morris & DeShon (2002), after first computing the variance of difference scores using reported N , M_{diff} and t values (see Supplementary Material S4). Paired correlations were estimated for the five effects for which the required data were available, however one was removed as it fell outside the possible range, leaving 4 correlations in total ($M = 0.81$, $SD = 0.31$). The mean of these correlations was then assumed for the remaining calculations of d_{RM} .

The standard error of each effect size estimate was calculated via the formula:

$$SE = \sqrt{\frac{1}{\frac{N+d^2}{2N}}} \quad \text{Equation 3.}$$

As in Equation 2, this SE formula was multiplied by $\sqrt{2(1-r)}$ to correct for the paired correlation between conditions.

When relevant statistics (e.g. t or F statistics) were not reported in the text, the effect size was estimated, where possible, using means and standard deviations estimated from published figures, via ‘GraphClick’ software (Arizona Software Inc., 2010). Finally, if insufficient information was available from any source, the study was excluded from analyses.

2.4. Model and analysis decisions

Effect size data were analysed in a random effects model. This model assumes that studies are estimating independent, randomly sampled values of the population parameters, and it is tolerant to heterogeneity across effect sizes (Cumming, 2012). Total effect size heterogeneity was estimated using the standardised measure Cochran’s Q , while I^2 was used to estimate additional heterogeneity beyond that expected in a fixed effects model (Cumming, 2012). Parameter estimates were derived via restricted maximum likelihood estimation to minimise bias (Viechtbauer, 2005).

To statistically assess model coefficients, Wald-type chi squared tests were computed. The pseudo- R^2 statistic was used to quantify the heterogeneity across effect sizes that was explained by moderators (see Supplementary Material S5). The unstandardized regression coefficient (b) indicated the direction and magnitude of effects. Likelihood ratio tests were used to compare models (whose parameters were derived via maximum likelihood estimation), in order to identify moderators that made a significant contribution to explained

heterogeneity. All analyses were carried out in *R*, using the ‘metafor’ package (Viechtbauer, 2010).

2.5. Dependency among effect sizes

The number of included conditions (nested within samples) and the number of independent samples (nested within studies) were coded. In some cases, samples were exposed to many conditions, resulting in multiple effect sizes from a single group of participants. Collapsing the data across these effects would ignore important information. However, the contribution of multiple effect sizes by a sample introduces dependency in the data; the results of the meta-analysis can become biased towards the (correlated) effect size estimates due to a single unrepresentative sample. The influence of dependency was examined by creating multi-level models (Cheung, 2014) where conditions (level 2) were nested within their samples (level 3). This allowed us to determine whether there was a significant effect size dependency (i.e. whether a 3-level model provides a better fit than a 2-level model). In addition, we investigated the influence of dependency by creating resampled data sets that included one effect size from each independent sample. This allows an examination of the data under conditions where dependency is eliminated (Greenhouse and Iyengar, 1994).

3. Results

3.1. Summary of included data

In total, 29 studies were analysed, involving 229 participants across 37 independent samples, yielding 76 effect size estimates. Detailed information about each effect is available in the Supplementary Material S1. Two effect sizes were more than ± 3 SDs from the mean. However, removing these outliers reduced the overall effect size by only 0.04 and all

416 significant moderators remained significant. They were therefore included in the main
417 analysis. The coding for each moderator variable can be found in Table 1, and a summary of
418 moderator coding for each effect can be found in Supplementary Material S6.

419

420 Table 1

421 *Moderator coding*

Moderator	Type	Values	Description of variable	Descriptive Statistics*	Missing Cases
<u>Characteristics of adaptation stimulus</u>					
Type of motion (Section 1.2.1.1)	Categorical	1=Translational motion 2=Complex motion	The type of motion used for adaptation in the study. Complex motion refers to any case where motion direction varies across the stimulus (i.e. expansion, contraction, rotation and spiral motion.	k=76 N ₁ =46 N ₂ =30	0
Adaptation stimulus area (Section 1.2.1.2)	Continuous	1.89°-1256.39°	The total area (in degrees of visual angle ²) covered by the adaptation stimulus. Excluded those not reporting the size of a central blank square/ellipse, or if adapting stimulus shape was not clearly specified.	k=64 μ=158.87° σ=277.50° Range=1.89°-1256.39°	12
Eccentricity of adaptation stimuli (Section 1.2.1.3)	Continuous	0.07°-3.5°	The distance between fixation and the adaptation stimulus (in degrees of visual angle). Averaged across width and height of this space if they differed.	k=55 μ=1.03° σ=1.08° Range=0.07°-5°	21
Speed of adaptation stimuli (Section 1.2.1.4)	Continuous	0.6°/sec-8°/sec	The speed of the adaptation stimulus. Calculated tangential speed at average eccentricity for rotational motion.	k=45 μ=4.16°/sec σ=1.79°/sec Range=0.6°/sec-8°/sec	31
Duration of adaptation (Section 1.2.1.5)	Continuous	1 sec-90 sec	The duration of a single adaptation period within each trial.	k=66 μ= 40.11 sec σ=21.40 sec Range=1-90 sec	10
<u>Test stimulus characteristics</u>					
Static vs. dynamic test stimuli	Categorical	1=Static 2=Dynamic	The type of test stimulus used to measure the MAE.	k=76 N ₁ =44	0

(Section 1.2.2.1)					$N_i=32$	
<u>Experimental paradigm</u>						
MAE measurement (Section 1.2.3.1)	Categorical	1=Duration 2=Strength	The method of measuring the MAE. ‘Duration’ paradigms record the time until MAE cessation. The ‘strength’ category includes all other methods of MAE measurement (e.g. nulling, 2AFC).	$k=92$ $N_i=51$ $N_i=25$		0
MAE response (Section 1.2.3.1)	Categorical	1=Magnitude 2=2AFC	2AFC measures of the MAE require participants to select one response of two response options (e.g. test is moving left or rightward). All other methods are coded as ‘magnitude’ responses.	$k=76$ $N_i=64$ $N_i=12$		0
Attentional manipulation (Section 1.2.3.2)	Categorical	1 = Distractor 2 = Tracking	The paradigm for manipulating attention. Distractor paradigms (see Fig. 1b) divert attention from adapting motion with a centrally presented task. Attentional tracking (see Fig. 1c) involves attending to one of two superimposed motion directions.	$k = 76$ $N_i=70$ $N_i=6$		0
<u>Participant characteristics</u>						
Participant naivety (Section 1.2.4.1)	Categorical	1=Naïve 2=Other	‘Naïve’ refers to a subject group composed only of observers naïve to the research hypotheses. The ‘other’ category includes experienced-only samples, as well as mixed naïve and experienced subject groups.	$k=69$ $N_i=44$ $N_i=25$		7

* k refers to the number of effects; N indicates the number of effects for each condition

3.2. Overall effect size of attentional modulation of the MAE

Results of the meta-analyses are depicted in Fig. 2. A large effect of attention was found ($k=76$, $N=229$, $d_{att}=1.12$, 95% CI [0.87, 1.38], $p<.001$). A number of analyses were conducted to explore potential file-drawer effects (in which null effects are sometimes unpublished). Rosenthal's (1991) fail-safe N indicated that 7,767 additional, null studies would be required to reduce the pooled effect size to non-significance. The actual number of unpublished (negative effect) studies was estimated to be 7, using the trim and fill method, based on the symmetry of the data (Duval and Tweedie, 2000a, 2000b). Attentional modulation of the MAE remained significant when these (simulated) effects were included, reducing the effect by only 0.18. When any single contributing effect was removed, the pooled effect remained significant (leave-one-out analysis, range [1.07, 1.15], $ps<.001$). See Supplementary Material S7 for more details and figures.

Significant heterogeneity was found, $Q(75)=244.06$, $p<.001$. The I^2 statistic revealed that 75.35% of the heterogeneity could not be accounted for by sampling variance. In order to explain this heterogeneity, moderators were examined.

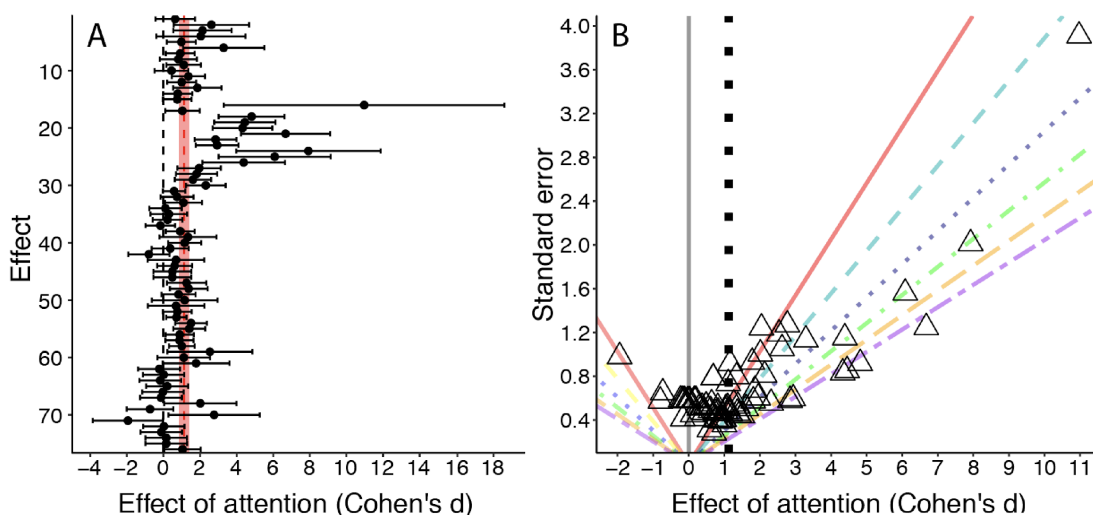


Fig. 2. Summary of the effect of attention on the MAE. a) Forest plot of all 76 effect sizes. Error bars are 95% confidence intervals. Red dashed line indicates the pooled summary

effect, surrounding shaded area depicts 95% CI. b) Funnel plot. Dashed line is the pooled effect size, coloured lines represent p values (Purple/Two-dash=.000001, Orange/Long-dash=.00001, Green/Dot-dash=.0001, Blue/Dotted=.001, Turquoise/Dashed=.01, Red/Solid=.05, Black=1).

3.3. Dependencies: overall analyses

A three-tiered model, nesting conditions within independent samples, was a better fit to the data than the two-tiered model $\chi^2(1)=34.69$, $p<.001$. This indicates dependence in the data – i.e. there is an effect of study. To characterise the influence of dependency on our global outcomes, the random effects model was applied to 500 resampled data sets, each of which contained one randomly selected effect size from each of our independent samples, yielding a total of 37 effect sizes for each data set. All subsets revealed a significant pooled effect (mean $d=1.01$, $SD=0.05$), indicating a strong attention-MAE relationship regardless of dependency.

3.4. Regression models with one moderator

A table summarising all single moderator regression models can be found in Supplementary Material S8. Important moderators (those that were individually significant or contributed to the best multiple regression model) are shown in Fig. 3. Motion type significantly affected the attentional modulation of the MAE ($Q(1)=17.43$, $b=-0.99$, $p<.001$), accounting for 24.92% of the total heterogeneity: studies using translating motion stimuli reported significantly larger effects than those using complex motion, (see Fig. 3a). However, attention had a significant effect on motion adaptation within the subset of studies using either translational motion, ($d=1.54$, $p<.001$) or complex motion ($d=0.56$, $p=.002$).

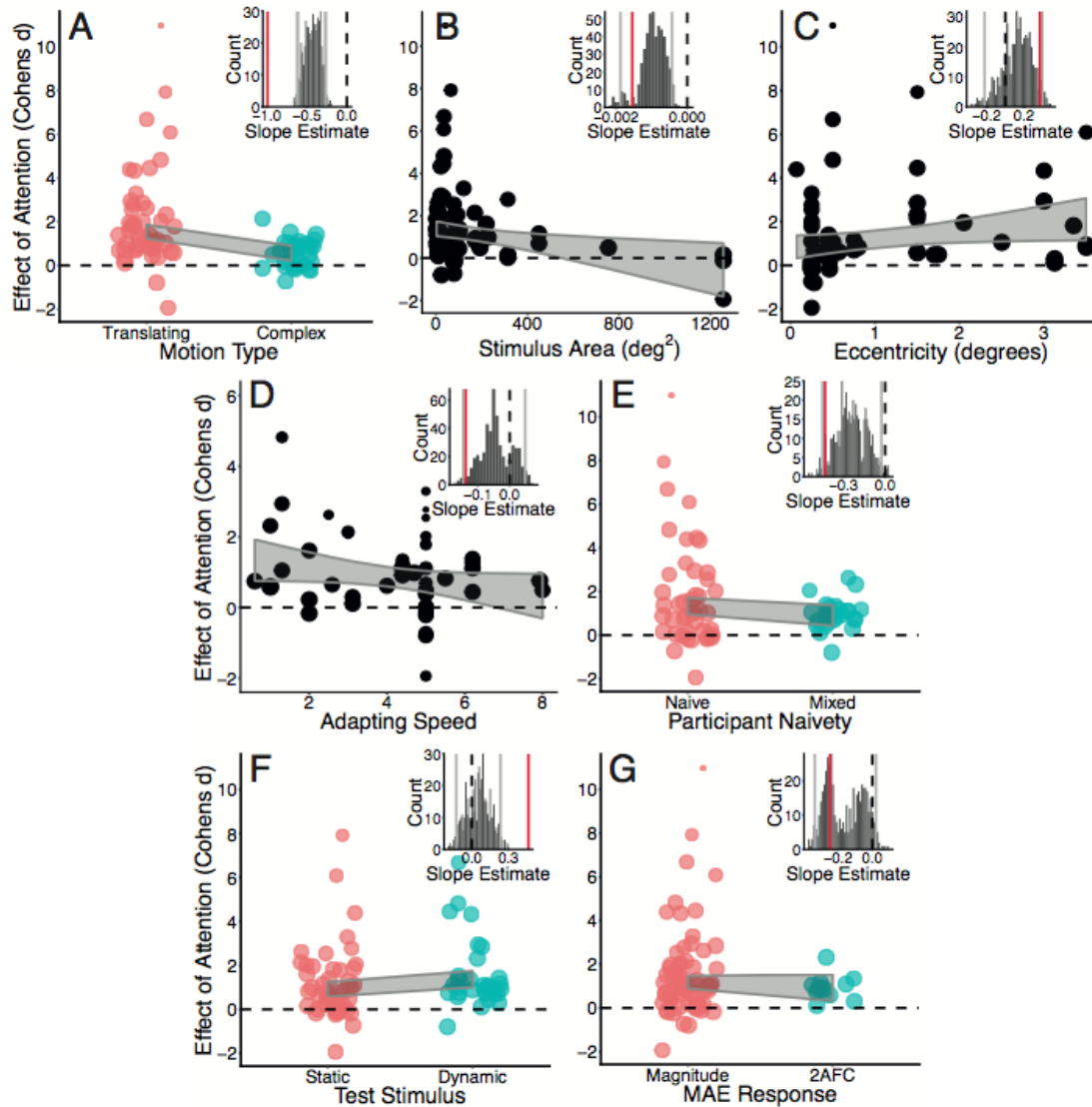


Fig. 3. Effect size summary for significant moderators (a-c) and factors that significantly contributed to the final model when considered alongside other moderators (d-g). The effect of attention (a) was larger for translational than complex motion, (b) decreased as stimulus size increased, (c) increased with greater eccentricity, (d) reduced with increasing adaptation speed, (e) was greater for naïve than mixed participant groups, (f) was greater for dynamic vs. static test stimuli, and (g) smaller when using a 2AFC response. Larger points indicate smaller standard error. The shaded ribbon indicates the 95% CI from the full dataset. Inset histograms detail the estimated slope parameter for 500 randomly selected datasets with dependency eliminated (see dependency information); red lines indicate estimated slope from

the full dataset; grey lines indicate the 95% CI determined by the resampled independent sample estimates; dashed black lines indicate the zero point.

The size (area) of the adaptation stimulus significantly affected attentional modulation of the MAE, $Q(1)=7.40$, $b=-0.002$, $p=.007$, accounting for 11.38% of the heterogeneity in the effect (see Fig. 3b). As stimulus size increased, the magnitude of attentional modulation decreased. In addition, there was a significant effect of the eccentricity of the adapting stimulus, accounting for 8.59% of the total heterogeneity, $Q(1)=4.05$, $b=0.37$, $p=.044$ (see Fig. 3c). The effect of attentional manipulations on the MAE was larger for stimuli that were further from fixation.

When considered alone, the speed of the adaptation stimulus was not significant, $Q(1)=3.36$, $b=-0.14$, $p=.067$, accounting for 2.74% of total heterogeneity. However, motion speed did contribute to the final model (see below); slower stimuli resulted in stronger attentional effects (see Fig. 1d).

Participant characteristics (i.e. naivety) did not significantly moderate the attention-MAE effect in a single moderator model ($Q(1)=1.98$, $b=-0.43$, $p=.159$), but did contribute to the overall model, with larger effects reported for studies using naïve participants. (This was not driven by a relationship between sample size and sample type – see Supplementary Material S9). Significant effects of attention on motion adaptation were found within the subset of studies using naïve participants ($d=1.33$, $p<.001$) and within those using experienced, or a mix of naïve and experienced, samples, ($d=0.90$, $p<.001$; see Fig. 3e).

The effect of test stimulus (static vs. dynamic) did not reach significance when considered alone ($Q(1)=3.29$, $b=0.46$, $p=.070$) but did contribute to the best complete model (see below). Using a static test stimulus to assess the MAE resulted in a weaker, though still

significant, effect of attention ($d=0.91$, $p<.001$) than using dynamic tests ($d=1.37$, $p<.001$).

This accounted for 7.12% of effect size heterogeneity (Fig. 3f).

The response paradigm made little difference to the measured effect of attention on the MAE. The effect size was similar across studies that measured the MAE duration vs. its strength ($Q(1)=0.49$, $b=0.19$, $p=.485$) with studies employing either method reporting significant effects (MAE duration: $d=1.06$, $p<.001$; MAE strength: $d=1.24$, $p<.001$). Further, effect size was not significantly modulated by whether a 2AFC design was used vs. a magnitude estimation method ($Q(1)=0.52$, $b=-0.25$, $p=.470$), although the stronger attentional modulation for magnitude designs compared to 2AFC designs contributed to the final model. Both subsets of studies produced significant effects of attention on the MAE (2AFC: $d=.93$, $p=.003$; magnitude estimation: $d=1.17$, $p<.001$, see Fig. 3g).

Neither the speed nor the duration of adaptation stimulus significantly affected the attention-adaptation relationship (see table in Supplementary Material S8). Finally, a significant effect of attention was reported within studies that used distractor paradigms (as depicted in Fig. 1b: $d = 1.12$, $p<.001$) as well as those that used attentional tracking paradigms (Fig. 1c; $d=1.18$, $p=.010$). The effect size was similar across both (no significant effect of attention paradigm: $Q(1)=0.01$, $b=0.06$, $p=.904$).

As described above, the effect of dependencies was explored via resampling. The distribution of regression coefficients across the 500 resampled sets of independent data can be seen in inset histograms of Fig. 3. Analysing these reduced datasets (with dependencies eliminated) reveals the same set of significant moderators. However, note that the regression coefficient for motion type (translational vs. complex) is larger when estimated from the complete data set than when estimated from reduced datasets. Some of the larger effect sizes for translational motion were produced from samples contributing multiple effects. Thus, we can be confident that studies with translating motion provide substantially larger effect sizes

than those using complex motion, but the estimated magnitude of this difference may be inflated by dependencies across estimates from common subject groups.

Selected two-way interaction analyses were conducted, however none of these reached significance (see Supplementary Material S10).

3.5. Multiple regression models

Multiple regression was used to determine the best-fitting model that incorporates multiple factors that contribute significantly to heterogeneity in effect size. A backward elimination strategy was implemented: starting from a model containing all complete effect moderators (those reported for every effect), moderators that did not significantly improve the model were eliminated in a step-wise fashion. We switched to Maximum Likelihood estimation to facilitate model comparison via likelihood ratio tests (*LRT*). Moderators were assessed in order of significance value, such that the moderator with the largest *p* value was considered first. Moderators were eliminated when their removal was associated with a non-significant decrease in the goodness of fit of the model, as determined by model comparison via *LRT*. Subsequently, reduced effect moderators (those reported for a subset of effects only) were considered individually and included only if they significantly improved the model. Those with the largest *N* were assessed first, to maximise the number of cases in the final model.

3.5.1. Complete effects

The initial model included all moderators for which values were available for all effects: type of motion (translation vs. complex), MAE measurement (duration vs. strength), MAE response (magnitude vs. 2AFC), test stimulus (static vs. dynamic) and attention paradigm (distractor vs. tracking). Through backward elimination, the optimal complete

effects model included motion type, MAE response and test stimulus as predictors. This model accounted for 42.05% of the heterogeneity of the effect of attention on motion adaptation.

3.5.2. Reduced effects

The complete effects model was significantly improved by adding four reduced effect moderators. The addition of each one decreases the number of effect sizes (k) included in the model. These reduced effects were participant naivety ($k=69$), stimulus area ($k=57$), eccentricity ($k=50$) and adaptation speed ($k=31$). The final model accounted for 63.18% of the heterogeneity of the effect; it is shown in Fig. 4 and summarised in Supplementary Material S11.

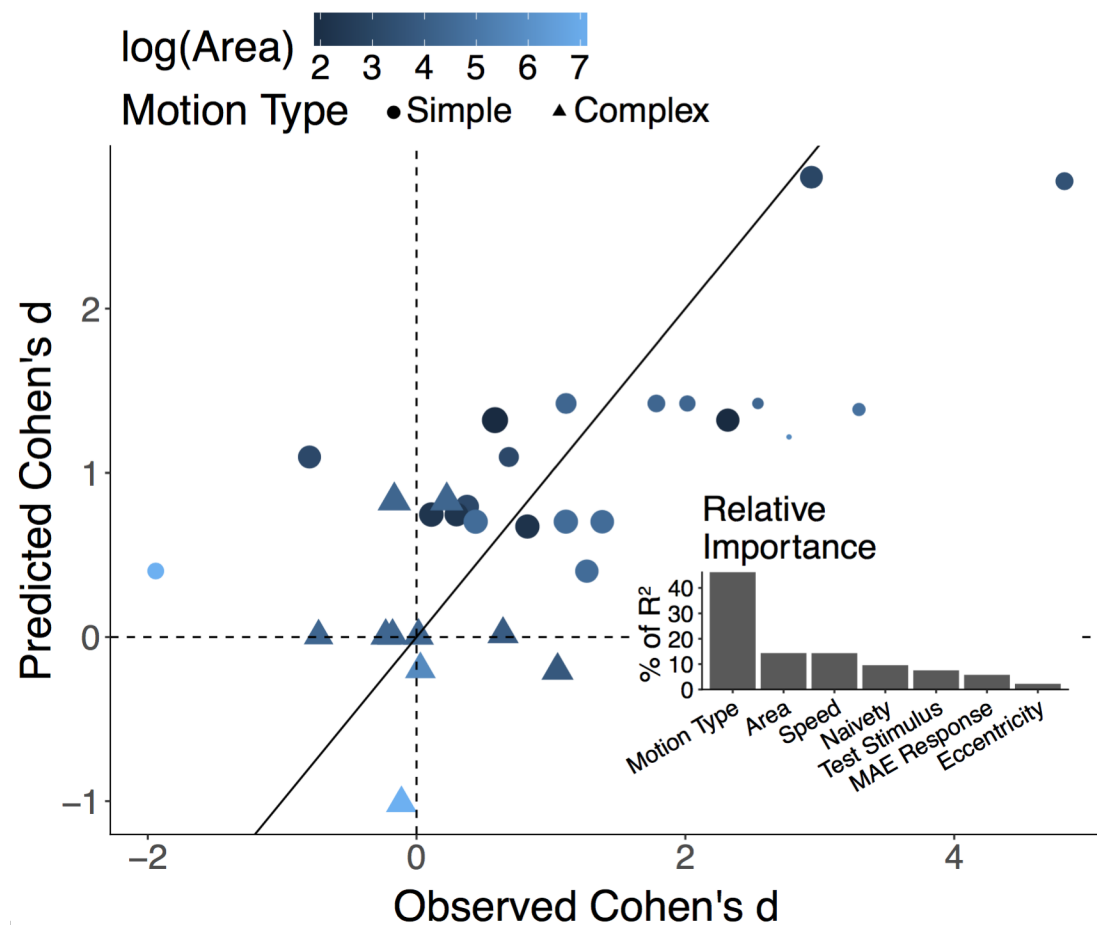


Fig. 4. Predicted Cohen's d_{av} values as a function of observed Cohen's d_{av} for each effect size

in final model. Size of the points indicates standard error; larger points have a smaller standard error. Inset: The relative importance of each factor in the final model. This is quantified by the pseudo R^2 statistic (see Supplementary Material S5), averaged across all possible orderings of regressor input (Lindeman et al., 1980).

4. Discussion

4.1. Summary of Findings

Attending to a moving stimulus significantly increases the resultant MAE. This effect of attention is modulated by various characteristics of the adaptation and test stimuli: larger attentional effects were found following adaptation to stimuli that were (i) translating (vs. those with complex motion trajectories) (ii) at a greater eccentricity and (iii) smaller in size. In addition, when considering multiple moderators simultaneously, stronger attentional modulation was reported in studies that employed dynamic, rather than static test stimuli, those using slowly moving adaptation stimuli, and those that used magnitude estimation, rather than 2AFC judgements to quantify the MAE. Further, greater attentional effects were reported in studies using exclusively naïve participants.

4.2. Discussion of adaptation and test stimulus characteristics

4.2.1. Type of motion

The effect of attention on motion adaptation was around twice as large for translating motion than for other motion patterns. This behavioural finding suggests that feature-based attention plays a substantial role in increasing motion adaptation. Although translational motion produced substantially stronger attentional effects, adaptation to complex motion was also significantly enhanced by attention. When considered alongside neurophysiology and fMRI evidence, the substantial difference between simple and complex motion suggests that

surface-based attention may drive some attentional modulation of activity within V1 / MT, but that this effect is small compared to the effects of simple feature-based attention. In addition, we know that neurons in MST can be tuned to large field translating, rotating or expanding / contracting patterns (Smith et al., 2006; Wall et al., 2008). The relatively small effect of attention on adaptation to complex motion therefore also suggests that attentional effects on adaptation within MST are small compared to those in V1/MT.

Early fMRI studies reported a significant effect of attending to complex motion in MT/MST but found no significant effects of attention in V1 (Büchel et al., 1998; O’Craven et al., 1997; Watanabe et al., 1998). It is possible that the effects of surface-based attention in V1 are relatively weak and hard to detect. Alternatively, V1 facilitation in a subset of neurons may have been masked by suppressive effects within neurons tuned to unattended motion directions. Facilitatory and suppressive effects of attention (in response to translating stimuli) have recently been revealed in V1 using more sophisticated, voxel-based analyses (Saproo and Serences, 2014), consistent with our findings.

4.2.2. Stimulus size

Our analyses revealed a relationship between stimulus size and the effect of attention, with a smaller effect for larger adaptation stimuli, in line with Takeuchi and Kita (1994). They suggested that small vs. large (or whole field) stimuli are processed by separate motion mechanisms, with the former sensitive to object motion, and the latter sensitive to the optic flow generated by self-motion. Our analyses revealed smaller attentional effects for larger adaptation stimuli (which may be processed as optic flow), consistent with the idea that selective attention affects the processing of object, rather than self-motion (Takeuchi & Kita, 1994).

We also considered whether the effect of stimulus size was driven by a confounding factor of eccentricity – smaller adaptation stimuli might, on average, be positioned further from fixation, allowing better control of spatial attention. Stimulus size was negatively correlated with eccentricity, but this did not reach significance ($r=-0.20$, $t(51)=-1.45$, $p=0.15$). Moreover, both stimulus size and eccentricity contributed significantly to the final model, suggesting that both factors are important in attentional modulation.

4.2.3. Eccentricity

Larger effects of attention were found for adaptation stimuli presented at greater distances from fixation. One plausible explanation for this relationship relates to our ability to control spatial attention: when we attend to a central task, the processing of nearby stimuli may also be affected – attention is not perfectly focussed on the central stimulus, but extends to proximal regions.

The positive relationship between eccentricity and the effect of attention on adaptation is in broad agreement with Lavie's (2005) load theory hypothesis - that an increase in load reduces the window of spatial attention.

4.2.4. Test stimuli

Some researchers have suggested that dynamic and static MAEs correspond to different motion mechanisms (e.g. Verstraten et al., 1996), which may differ in their susceptibility to attention. Our analyses show that attention affects MAEs measured with both dynamic and static test stimuli. Although larger effects were found with dynamic tests, this was a modest difference, that did not reach significance when considered alone and may be an artefact of dependencies within studies (see the resampling analyses in Fig. 3f).

4.2.5. *Adaptation speed*

Our analyses provide some evidence that the speed of the adaptation stimulus affects attentional modulation of the MAE, with a trend for weaker attentional modulation for faster adaptation stimuli. One possibility is that fast-moving stimuli capture attention, and thus attempts to divert attention are less effective.

4.3. *Factors related to response bias*

4.3.1. *Response type*

We considered whether the effects of attention on the MAE might be driven by, or inflated by, response bias. Asking observers to estimate MAE duration is considered more vulnerable to response bias (Morgan, 2013, 2012, 2011), whereas 2AFC tasks are considered less prone to criterion and / or bias effects. However, reported effect size was not significantly moderated by these factors (when considered in single predictor models). In fact, measures of MAE magnitude produced slightly larger estimates of the attentional effect than studies that asked observers to report MAE duration. Although the choice of 2AFC vs. magnitude estimation was not significant when considered alone, it did contribute to the final model, providing some evidence that 2AFC paradigms produce slightly more conservative (but still significant) estimates of the attentional effect.

4.3.2. *Participant characteristics*

If response bias does inflate estimates of the effect of attention, one would expect this to be an issue predominantly amongst non-naïve observers, who understand the attention hypothesis: for response bias to modulate effect size, observers should not only bias their responses in accordance with motion adaptation, but to systematically vary this bias as a function of attention condition. On the contrary, participant naivety did not reach significance

as a single moderator, and experiments using naïve subjects reported *larger* effects, with this effect contributing to the final model.

4.4. Nonsignificant moderators

A strong and significant effect of attention was found within both distractor and attentional tracking paradigms; both provide an effective manipulation of attention, and modulate the MAE to a similar extent. This contrasts with the suggestion that the two paradigms probe distinct attentional mechanisms, and that only attentional tracking paradigms modulate motion adaptation (Morgan, 2012, 2011). An alternative, supported by our analysis, is that attentional tracking paradigms have produced more consistent effects of attention because they tend to use translating motion stimuli (rather than expanding, or rotating motion).

Consistent with our previous research (Bartlett et al., 2018), adaptation duration did not significantly moderate attentional modulation of the MAE. Previously we examined whether attention affects the rate at which the MAE builds up, or the asymptotic MAE. We found that attention affects the MAE asymptote, rather than the timecourse of adaptation, and this finding is mirrored in our current analysis: comparable attentional modulation was discovered across the wide range of adaptation durations included in the surveyed literature.

Prior work has demonstrated that MAEs increase with adaptation duration (e.g. Bartlett et al., 2018). As discussed above, this duration-related increase in MAEs is not associated with increased attentional modulation. However, it is worth considering whether, more broadly, larger MAEs are associated with increased attentional modulation. Could it be that study designs that produce large MAEs (in terms of effect size) are more sensitive, and therefore also report greater effects of attentional modulation? Moreover, could MAE strength be a mediating variable that ‘explains’ the effects of some of our identified

moderators? To investigate this, we quantified baseline MAE strength (in the passive, or low-load condition) using Cohen's D . (Equation 1 reduces to the mean difference between a null result (i.e. no MAE) and the low-load / passive condition, divided by the low-load standard deviation). A small number of effects (12) were excluded from this analysis because an estimate of baseline MAE strength was not available. Within the remaining effects ($k=64$), MAE strength was not substantially or significantly related to the effect of attention ($Q(1)=0.20$, $b=-0.02$, $p=.655$). Further analyses confirmed that MAE strength did not significantly contribute to the final model, $LRT=0.06$, $p=.800$ ($k=57$). Thus, significant predictors of the modulatory effect of attention on motion adaptation (such as motion type, or stimulus size) cannot be 'explained away' via effects on baseline MAE strength.

4.5. Reconciling the literature

Attentional modulation of the MAE is a fairly robust effect: significant effects were found at each level of all categorical moderators. However, the strength of the attention effect is substantially moderated by a number of factors, with motion type (translating vs. complex) being the most important. Our multi-moderator model accounted for 63.18% of variation in effect size across studies.

Other, un-modelled factors will also contribute to apparent inconsistencies in the literature. For example, within the distractor paradigm, studies vary in how they manipulate attention; some 'high load' or 'diverted' attention conditions may be less effective than others in drawing attention away from the motion stimulus. However, this variability is hard to model, given the variety of tasks, and – in some studies – a lack of information about task difficulty / observer accuracy.

4.6. Relationship to neuroimaging

As described above, both monkey neurophysiology and human fMRI studies have provided evidence that attention modulates motion-related activity at multiple cortical regions, including V1, MT and MST. Although early work focussed on spatial attention, many studies have revealed effects of feature-based attention, and surface-based attention. Some have suggested that a unified attention system exists that treats stimulus location (and possibly object identity) as stimulus ‘features’, alongside motion direction (see Maunsell and Treue, 2006), although recent work suggests that spatial and feature-based attention may, in part at least, rely on different underlying neural mechanisms (Xue et al., 2017). Our meta-analysis suggests that simple, feature-based attention has much stronger effects on motion adaptation than spatial attention, or higher-level ‘surface-based’ attention: the largest effects of attention are seen for coherently translating stimuli, that maximise the effects of feature-based attention. This suggests a larger role for V1 and MT in attentional modulation of motion processing.

Attentional modulation decreased for larger stimuli at smaller eccentricities, conditions that may increase the extent to which spatial attention ‘spills over’ from a central task, to a peripheral motion stimulus. This makes sense if spatial attention modulates neuronal activity according to the extent of overlap between a neuron’s receptive field and the spatial locus of attention (Maunsell and Treue, 2006). Large-field stimuli will be particularly effective in driving activation in MSTd, where receptive fields are large and more will overlap with a central attended region of visual space.

We compared the effect of attention on MAEs measured with dynamic and static test stimuli. Previous authors have shown greater interocular transfer of the dynamic MAE (Nishida et al., 1994) and suggested that static MAEs predominantly reflect adaptation in V1, whereas dynamic MAEs also involve MT (Mather et al., 2008). Our findings are broadly

consistent with this suggestion – the larger effect of attention on the dynamic MAE may reflect attentional modulation across V1 and MT/MST.

5. Conclusions

Our meta-analysis supports a number of conclusions. First, there is overwhelming evidence that motion adaptation is affected by attention. By analysing the effects of different paradigms, participant naivety and looking for evidence of the ‘file drawer’ effect, we can be confident that reported effects are not driven by response bias or publication bias. It seems that Wohlgemuth (1911) was wrong after all. More importantly, we identified several factors that modulate the effects of attention on motion adaptation, allowing us to explain some apparent inconsistencies in the literature. Our analyses suggest that the largest effects of attention on motion adaptation will be seen for studies that use translating motion stimuli, within either attentional tracking paradigms, or ‘distraction’ paradigms, particularly when the adaptation stimuli are some distance from fixation. These design choices are likely to exploit (direction-specific) feature-based attention, largely reflected in V1 and MT modulation that includes both facilitation and suppressive effects. However, some additional attentional modulation is likely to be driven by surface-based attention and (for ‘distraction’ paradigms) spatial attention.

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